The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

(Article begins on next page)

05 May 2024

The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

Susanne Jähnig[1]*, Riccardo Alba[1], Cristina Vallino[1], Domenico Rosselli[2], Marco Pittarello[3], Antonio Rolando[1] & Dan Chamberlain[1]

[1] Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123, Turin, Italy.

[2] Ente di Gestione delle Aree Protette delle Alpi Cozie, Via Fransuà Fontan 1, 10050 Salbertrand, Italy.

[3] Department of Agricultural, Forest and Food Sciences, University of Turin, Largo Paolo Braccini 2 ,10095 Grugliasco, Italy.

*Corresponding author

Tel: +39 333 918 2681

Email: susanne.jaehnig@gmail.com

Abstract

In a mountain context, the forest-shrub ecotone is an area of high biodiversity. Relatively little is known about the habitat requirements of birds in this habitat, yet it is facing potential threats from changes in grazing practices and climate change. Moreover, it is not clear at which scale habitat associations should be assessed in Alpine birds. Further information on key habitat components affecting bird communities of the ecotone are needed in order to inform management strategies to counteract potential habitat loss, and to better inform predictions of how bird communities may be affected by future environmental change. Data on bird occurrence and broadscale (land cover) and finescale (vegetation structure and shrub species composition) habitat variables were collected in an Alpine forest-shrub ecotone in Val Troncea (northwestern Italian Alps) in order to address two objectives: to identify the key habitat variables associated with the occurrence of individual species and with the diversity of the bird community; and, to assess which scale of habitat measurement (broadscale, finescale or both combined) is needed to model bird occurrence. Broadscale variables, or combinations of broad- and finescale variables, tended to have the best performing models. When combined models performed best, shrub species identity was included in many cases. Shrubs also played an important role in explaining variations in species diversity and richness. Vegetation structure was of relatively little importance, either for individual bird species or for species richness and diversity. These findings suggest that management should strive to maintain a mosaic of habitats whilst minimizing forest encroachment, which could be achieved through targeted grazing. Broadscale habitat data and data on shrub species composition should provide a sufficient basis for identifying relevant species-specific habitat parameters in a mountain environment in order to model future scenarios of effects of habitat change on the bird community of the alpine forest-shrub ecotone.

Introduction

Mountain biodiversity is under a range of environmental pressures, including land use change (Laiolo et al. 2004), increased human leisure activities (Rolando et al. 2007; Arlettaz et al. 2007), climate change (Sekercioglu et al. 2008; Dirnböck et al. 2011), and interactions between these factors (e.g. Brambilla et al. 2016). Climate change may be a particular problem given that the rate of warming in mountains is approximately double the global average, a trend that is expected to continue (Böhm et al. 2001). A consequence of climate change is that vegetation zones are likely to shift upwards – for example, the upper forest limit has shifted to higher elevations in many mountain regions in line with rising temperatures (Harsch et al. 2009). The loss of high altitude open habitats as a consequence of such vegetation shifts has been identified as a potential future conservation problem (Sekercioglu et al. 2008; Chamberlain et al. 2013), especially as the proportion of species of conservation concern tends to increase with elevation (Viterbi et al. 2013). However, vegetation shifts in some areas have also been due to abandonment of grazing which maintained the forest limit at a lower altitude than would be possible under only climatic constraints. This effect has had a greater effect than climate change on treeline shifts in the European Alps (Gehrig-Fasel et al. 2007).

The ecotone between the forest and the alpine grassland zone is characterized by a high structural diversity, typically being a mix of open grassland areas, pioneer forest and shrub species. It is therefore often an area of high biodiversity (Dirnböck et al. 2011). Whilst abandonment of grazing and vegetation shifts due to climate change may, at least initially, have the capacity to create new habitats, in particular through the colonization by shrub species (Laiolo et al. 2004), there are also threats to this habitat. First, it seems plausible to expect that structural diversity is a key factor driving the relatively high biodiversity of the ecotone (e.g. MacArthur and MacArthur 1961), and grazing is likely to maintain a habitat mosaic that underpins the structural diversity, hence further abandonment of grazing may be detrimental. Second, many mountainous areas do not reach altitudes that are high enough

93   to maintain the ecotone habitat given the likely magnitude of vegetation shifts (Dirnböck et

94   al. 2011) – such areas are likely to be mostly forest in the future. Third, it cannot be assumed

95   that all components of the vegetation community will respond simultaneously to climate

96   change (Theurillat and Guisan 2001). For example, there is evidence that vegetation zones

97   respond differentially to warming temperatures in the Alps (Cannone et al. 2008), and that

98   trees and shrubs may respond differentially to reduced snow cover resulting from climate

99   change. Snow has insulating properties that benefit some shrub species from frost damage

100 (Neuner 2014), and lower snow cover or earlier snow melt could potentially lead to a net loss

101 of ecotone habitat.

102   Within the gradient of alpine habitats from mountain forest to the highest altitude nival

103 zone (Kapos et al. 2000, Körner & Ohsawa 2006), the highest biodiversity is typically found

104 in the forest-shrub ecotone, yet it has been little studied in an avian context. Whilst common

105 species such as Dunnock *Prunella modularis*, Linnet *Carduelis cannabina*, Lesser

106 Whitethroat *Sylvia curruca* and Wren *Troglodytes troglodytes* have been studied in lowland

107 habitats (usually at higher latitudes), the few studies that have assessed habitat associations

108 in these species in mountain habitats have considered only broadscale, usually remote-

109 sensed, habitat data and have not considered more detailed measures of habitat complexity

110 (Chamberlain et al. 2013, 2016). With a few exceptions, notably Black Grouse *Tetrao tetrix*

111 (e.g. Patthey et al. 2012, Braunisch et al. 2016) and Ring Ouzel *Turdus torquatus* (von dem

112 Bussche et al. 2008), there is as yet insufficient information to determine at which scale

113 species-habitat associations should be assessed in order to plan conservation actions for

114 the majority of common Alpine ecotone species in the context of environmental changes.

115 Furthermore, such studies would also allow the improvement in our ability to forecast

116 potential effects of future environmental change for ecotone species. Species distribution

117 models for typical ecotone species such as Dunnock, Wren and Tree Pipit *Anthus trivialis*

118 show generally less good model performance, and greater inconsistency in model outcomes

119 between different scenarios of change, compared with forest and grassland species

120 (Chamberlain et al. 2013, 2016). This may be because these species are more dependent

121   on finescale habitat characteristics, such as vegetation structure, and hence are not well-

122   described by land cover and topographic variables that typically underpin many species

123   distribution models.

124   Heterogeneity plays an important role for bird species diversity in a range of different

125   habitats, including farmland (Benton et al. 2003), rain- (Guerta and Cintra 2014) and

126   temperate forests (Freemark and Merriam 1986) and grasslands (Hovick et al. 2014).

127   However, the role of heterogeneity in the forest-shrub ecotone is still not well understood.

128   We would expect that, based on the influence of habitat diversity and structural vegetation

129   diversity, species richness in the ecotone would be positively associated with measures of

130   habitat heterogeneity. A recent study on Black Grouse in the Swiss Alps showed that

131   horizontal and vertical structural heterogeneity was the best predictor for the occurrence of

132   the species (Patthey et al. 2012). We similarly expect that ecotone species will in general be

133   positively associated with habitat complexity. In this study, we consider complexity in terms

134   of the diversity of vegetation structure, the heterogeneity in vegetation height, and also in

135   terms of the habitat mosaic formed by shrubs, grassland and forest. We focus in particular

136   on non-linear relationships between the bird community and shrub cover as a measure of

137   the habitat mosaic, the expectation being that bird diversity and individual species

138   occurrences will peak at intermediate values of shrub cover.

139   The specific objectives of this study are (i) to assess key habitat attributes that

140   influence bird diversity and individual species occurrence in an Alpine forest-shrub ecotone,

141   and (ii) to determine whether habitat cover and altitude are adequate to model species

142   distributions in the ecotone, or if more detailed information on vertical vegetation structure

143   and shrub species composition is needed.

144

145   **Methods**

146   **Study area and point selection**

147 The study was carried out in Val Troncea Natural Park (44°57'28" N; 6°56'28" E) in the

148 western Italian Alps. At lower altitudes the area is dominated by larch *Larix decidua*. The

149 natural treeline is typically found at around 2200 m asl, but varies depending on local

150 conditions. Typical shrub species are *Juniperus nana* (henceforth Juniper) and

151 *Rhododendron ferrugineum* (henceforth Rhododendron) which rapidly encroached wide

152 areas of grasslands after the decline of agro-pastoral activities. Grasslands were mainly

153 dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky

154 areas occur predominantly at higher altitudes, above approximately 2700 m asl.

155   Point counts were carried out in the forest-shrub ecotone, which we defined as the

156 transition zone between forest and alpine grasslands. We included both natural ecotones

157 where the treeline is limited by climatic conditions, and areas where open grassland has

158 been maintained at lower altitudes, mostly due to grazing by domestic livestock, but also due

159 to avalanches in some locations. Point count locations coincided with the centroids of a pre-

160 existing grid at a scale of approximately 150 x 150 m (there was some variation, due to

161 access constraints for example; Probo et al. 2014) along the western facing slope of the

162 valley. Points were selected that had a minimum shrub cover of 5 % and a maximum tree

163 cover of 70 % (i.e. thus presenting the forest-shrub ecotone) within 100 m radius according

164 to vegetation surveys (see below). All points were spaced a minimum of 200 m apart.

165

166 **Bird surveys**

167 Point counts (n = 79) were carried out from mid-May to mid-July over a period of 2 years (46

168 in 2015 and 33 in 2016) following the methods of Bibby et al. (2000), using a 10 minute

169 count period. At each point count location, all individual birds seen or heard were recorded

170 within a 100 m radius (estimated with the aid of a laser range finder). Point counts

171 commenced 1-1.5 h after sunrise and continued until 1200 h. Surveys did not take place in

172 excessively wet or windy conditions. Each point count location was visited once.

173

174 **Broadscale and finescale habitat**

175 Habitat data were defined into two categories representing 'broadscale' habitat data (land

176 cover, altitude and other variables estimated at a resolution of the whole point count

177 location) and 'finescale' habitat data (vegetation structure and shrub species composition

178 estimated from plots at a finer scale of resolution within the point count location). Broadscale

179 habitat comprised visual estimation of the percentage cover of canopy (i.e. vegetation above

180 head height), shrubs (woody vegetation below head height), open grassland and bare rock

181 (including scree and unvegetated areas) within a 100 m radius of the point's centre. The

182 number of mature trees (greater than c. 20 cm in diameter at breast height) within a 50 m

183 radius of a point count location was also counted. These estimates have been shown to

184 correlate well with estimates of land cover derived from remote sensing and have been used

185 as the basis of predictive models for several species considered here (Chamberlain et al.

186 2013, 2016).

187 Finescale habitat data on vegetation structure and composition were collected at the

188 centre of the point count location and along two 100 m long transects, each divided into 5

189 plots spaced 20 m apart originating at the point's centre (therefore there were eleven plots

190 sampled per point count location including the central point). The compass bearing of each

191 transect from the centre of the point to its perimeter was selected at random, the only

192 constraint being that there had to be an angle greater than 90° between two transects at the

193 same point. Following Bibby et al. (2000), at each plot, vegetation density was measured at

194 three different heights (0 m; 0.5 m; 1 m) using a chequered board (50 cm x 30 cm), divided

195 into 10 x 10 cm square subdivisions, placed vertically into the vegetation, the bottom of the

196 board coinciding with the appropriate height class. To produce an index of vegetation

197 density, an estimate was made of the number of squares of the board that were obscured by

198 vegetation observed from a distance of 5 m. A square was considered obscured by

199 vegetation when <50 % of it was visible. The diversity of vegetation density over all 11 plots

200 was then calculated with the Shannon index $H' = -\sum p_i \ln p_i$, where p_i is the proportion of

201 squares obscured at the ith plot. Data were also collected on grass and shrub height (if

202 present), and the standard deviation of height calculated across the 11 plots was used as a

203 measure of vegetation height heterogeneity for each point. The dominant shrub species at

204 each plot within a 1 m radius was recorded, defined into four groups: Rhododendron,

205 Juniper, bilberry (*Vaccinium myrtillus and V. gaultherioides)* and other (e.g. Green Alder

206 *Alnus viridis,* Willow *Salix spp,* and also including young trees less than two meters in height,

207 mostly European Larch *Larix decidua*). The frequency of plots in which a given group was

208 present was calculated for each point (i.e. the maximum frequency was 11). All habitat

209 variables used in the analysis are listed in Table 1 (a complete list of variables measured in

210 the field, but not included in the models due to collinearity, are given in Electronic

211 Supplementary Material (ESM) Table S1).

212

213 **Data analysis**

214 Birds detected within a 100 m radius of a point count location were used to analyse species

215 richness (simply the number of species detected on each point count), species diversity

216 (expressed using the Shannon index) and species distribution (presence/absence of

217 individual species) with regard to habitat composition and structure within the forest-shrub

218 ecotone.

219 Data were analysed using an information theoretic approach with the MuMIn package

220 in R (R v.3.3.2, R Development Core Team 2016; Bartoń 2013). This entailed first deriving

221 full models at each scale and for each dependent variable (richness, diversity or species

222 presence) using a mixed modelling approach in the R package lme4 (Bates et al. 2015).

223 Model-averaged parameter estimates were derived for all combinations of variables in each

224 full model in order to identify variables that were most closely associated with bird

225 distribution and diversity. P-values derived from the model-averaged parameter estimates

226 and their standard errors were considered to represent significant effects when P < 0.05. In

227 addition, the Akaike Information Criterion corrected for small sample size (AICc) was

228 determined for each individual model and was used to assess model performance at

229 different scales (see below).

230   Prior to modelling, all variables within each set (i.e. broad- or finescale) were scaled

231 and centred. Variance inflation factors (VIFs) were calculated using the 'corvif' function

232 (package 'AED', Zuur et al. 2009) to assess collinearity between continuous explanatory

233 variables. All variables with a VIF > 3 were sequentially removed from the variable set until

234 all VIFs were < 3. Intercorrelations between remaining variables were then checked, and for

235 those with Spearman correlation coefficients > 0.50, one of the pair was subsequently

236 omitted (variables with a large proportion of zeroes were preferentially omitted, otherwise the

237 choice was random). As a final check, variables that had been removed in the procedure to

238 minimise collinearity were substituted for closely correlated variables (in particular between

239 overall shrub cover or frequency, and the frequency of individual shrub species). Cases

240 where the model with the substituted variable had a lower AICc were used in the final full

241 model. As we were particularly interested in how the shrub-grassland habitat mosaic

242 affected the bird community, we included a quadratic effect of variables representing shrub

243 cover (including the frequency of individual shrub species) in all models. For other variables,

244 non-linear effects were included in the models following visual assessment of scatterplots

245 (following Zuur et al. 2009). Year was specified as random effect in every model to account

246 for possible inter-annual effects.

247   Species richness and species diversity were analysed using generalised linear mixed

248 models in relation to habitat variables, specifying a Poisson and a normal error distribution

249 respectively. The occurrence probability of the commonest species (present on 15 % of

250 points – Chamberlain et al. 2013 found that models performed persistently poorly below this

251 threshold) in relation to habitat was analysed using binomial logistic regression, each

252 species being recorded as either present or absent per point. At each scale, the residuals for

253 all full models were extracted and tested for spatial autocorrelation using Moran's I (Moran

254 1950). There was no strong evidence of spatial autocorrelation across species or scales

255 (see details ESM Table S6 and S7), therefore this was not considered further.

256   At the end of the above process, for species richness and diversity and for each

257 individual species, candidate models with model averaged parameter estimates were

258   derived for each combination of variables based on the full model for broad- and finescale

259   habitat variables separately. The next step was then to derive combined models based on

260   the most important variables from both broadscale and finescale models, defined as those

261   variables which were either significant ($p \leq 0.05$) or which approached significance ($p \leq 0.1$)

262   from the broad- and finescale model sets. In the few cases where no variables had $P < 0.10$,

263   those with a high Akaike weight (> 0.50) in each scale-specific model were used in the

264   combined model. The new data set was again subject to variable set reduction according to

265   VIFs and correlation coefficients, and subsequently combined models were derived, which

266   were again subject to model averaging.

267   The extent to which broadscale or finescale habitat structure, or a combination of the

268   two, was necessary to model species diversity and distributions was assessed using AICc.

269   At each scale (finescale, broadscale and combined) and for each dependent variable,

270   models were ordered according to the AICc, where lower values indicate better performing

271   models. Change in AICc relative to the top ranked model was calculated as ΔAICc. Models

272   with ΔAICc < 2 were considered equivalent. Models from all three scales were compared in

273   order to assess whether high model performance was associated with either broadscale or

274   finescale habitat variables, or a combination of both. The importance of each variable at

275   each scale was assessed by calculating Akaike weights based on all combinations of

276   models (Burnham and Anderson 2002), which are expressed as the likelihood contribution of

277   each model as a proportion of the summed likelihood contributions of all models. The weight

278   for each variable is the sum of model weights for all models in which a given variable was

279   present (Burnham and Anderson 2002).

280

281   **Results**

282   In total, 263 individuals of 29 species were recorded in 79 point counts over an altitudinal

283   range of 1800-2600 m asl. There were eight species that were recorded on at least 15 % of

284   the points: Tree Pipit, Water Pipit *Anthus spinoletta*, Dunnock, Northern Wheatear *Oenanthe*

285 *oenanthe*, Lesser Whitethroat, Wren, Chaffinch *Fringilla coelebs*, Rock Bunting *Emberiza*

286 *cia*. No significant model averaged parameter estimates could be identified to predict Rock

287 Bunting occurrence for broad- or finescale models, therefore this species was not

288 considered in further analyses.

289

290 **Broadscale habitat structure**

291 Details of model-averaged parameters of the model set for broadscale habitat structure are

292 given in ESM Table S2. Bird species richness and diversity showed a positive relationship

293 with the number of mature trees. Shrub cover showed a quadratic effect on bird diversity

294 whereby diversity increased initially with the percentage of shrub cover, but declined after a

295 shrub cover of approximately 55 % was reached. Furthermore, diversity was negatively

296 associated with altitude. Among individual species, Dunnocks showed a positive linear

297 association with shrub cover, whereas both Lesser Whitethroat and Wren showed a

298 quadratic association, where the probability of occurrence of Lesser Whitethroat and Wren

299 peaked at c. 45% and c. 50% shrub cover respectively. The number of mature trees showed

300 a positive relationship with Chaffinch presence. There was also a negative effect of rock

301 cover on Tree Pipit occurrence. Altitude was the only variable within the full model which

302 was not linked to vegetation cover, and had different effects on the occurrence probability of

303 Chaffinch, Wren (negative) and Northern Wheatear and Water Pipit (positive).

304

305 **Finescale habitat structure**

306 Details of model-averaged parameters of the model set for finescale habitat structure are

307 given in the ESM Table S3. A number of dependent variables showed significant quadratic

308 effects (e.g. probability of occurrence or diversity peaking at intermediate frequencies), either

309 for all shrubs (Northern Wheatear), or for individual shrub species (Wren and Juniper

310 frequency, Dunnock and Rhododendron frequency, species diversity and Bilberry

311 frequency). Shrub height heterogeneity was positively correlated with Wren and Tree Pipit

312 presence. A positive relationship of canopy presence was found for bird species richness

313   and diversity, as well as for Chaffinch presence. In contrast, it showed a negative

314   association with Northern Wheatear presence. Structural vegetation diversity was not

315   selected in any model set (see ESM Table S3).

316

317

318   **Combination of broadscale and finescale habitat structure**

319   Details of significant model-averaged parameters of the final combined model sets are given

320   in Table 2 (for a full list of parameters see ESM Table S4). In line with our expectation on

321   effects of habitat mosaics on ecotone species, we here focus on shrub cover, but graphs of

322   all significant variables in combined models are presented in ESM, Fig. S1. Shrub cover, as

323   a broadscale variable, occurred in the combined model set for bird species diversity (Fig. 1)

324   and Lesser Whitethroat (ESM Fig. S1). In a number of cases, individual bird species

325   occurrences were closely associated either with shrub species identity or with shrub

326   frequency (Table 2). Quadratic relationships between shrub species and bird species

327   occurrence were found for Dunnock (Rhododendron), Wren (Juniper) and bird species

328   diversity (Bilberry, see Fig. 2). Tree Pipit occurrence declined with increasing Rhododendron

329   frequency (Fig. 2). Shrub height heterogeneity was closely related to Tree Pipit and Wren

330   occurrences.

331   The frequency of canopy or the number of mature trees was retained in the combined

332   models for bird species diversity, bird species richness and Chaffinch occurrence (positive

333   associations) as well as for Dunnock occurrence (negative association). Altitude showed a

334   negative relationship with the occurrence of Wren and Chaffinch, while it was positively

335   associated with Northern Wheatear presence.

336

337   **Model comparison**

338   A summary of the ten highest ranked models for each species and each diversity measure

339   across scales is shown in Fig. 3. The higher ranked models were mostly based on combined

340   models (i.e. combinations of broad- and finescale variables), or broadscale models alone.

341 The best models (ΔAICc < 2) for Dunnock, Lesser Whitethroat, Northern Wheatear, Tree

342 Pipit, Chaffinch, Wren and species diversity contained only combined models. Finescale

343 models were in the best model set only for species richness, but combined and broadscale

344 models performed equally well (i.e. ΔAICc < 2). Figure 3 also illustrates that, for many

345 species, there was a high degree of model uncertainty in that there were often several

346 models where ΔAICc < 2. In general, finescale habitat variables of high weight that were

347 present in the combined (best) models were related to the presence of shrubs either overall

348 (Northern Wheatear) or of specific shrub species (Dunnock, Lesser Whitethroat, Tree Pipit,

349 Wren and bird species richness and diversity; Table 3).

350

351

352 **Discussion**

353 The aim of this study was to describe species-specific habitat requirements within a

354 mountainous forest-shrub ecotone in order to assess the relationships between the diversity

355 and distributions of birds and environmental variables measured at different scales, and

356 hence to identify potential conservation priorities and to inform future modelling methods.

357 Through the combination of broad- and finescale habitat data in final models, we determined

358 key habitat characteristics which shaped bird species richness and diversity. Furthermore, it

359 enabled us to pinpoint habitat elements which are specifically required by common ecotone

360 species. Our expectations of positive associations between bird community measures

361 (diversity and individual species occurrence) and habitat complexity were partially met in

362 terms of shrub cover and to a lesser extent shrub height heterogeneity, but there was no

363 evidence that the diversity of vegetation structure was important.

364

365 **Comparison of model scales**

366 For making management recommendations, the identification of key habitat characteristics

367 (e.g. vegetation structure or plant species composition) supporting bird species diversity or

368 target species is essential. The decision at which scale this objective will be addressed

369 varies among studies representing a trade-off between broadscale (remote sensing

370 techniques, Braunisch et al. 2016) and finescale data collection (detailed vegetation

371 measurements in the field, Patthey et al. 2012). Both techniques show advantages and

372 disadvantages. Collecting broadscale data (for example, through remote-sensed data bases)

373 allows large areas to be covered, but has the potential to miss relevant habitat features.

374 Data collection in the field provides more detailed information, but is time consuming and

375 only applicable for smaller areas. Therefore choosing the appropriate scale is crucial as it

376 directly determines the outcome of the study. The model scale comparison (broadscale,

377 finescale or combined) applied on the same data allowed the assessment of the scale of

378 data collection needed to identify habitat parameters determining bird species diversity or

379 species specific habitat requirements in the forest-shrub ecotone.

380 The comparison revealed that combined and/or broadscale models always performed

381 better than finescale models for individual species. When combined models performed best,

382 variables linked to shrub species identity (finescale variables) were included in several cases

383 (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity).

384 Other finescale variables were rarely included in the combined model set for individual bird

385 species, or alternatively could be substituted by equivalent broadscale variables which had

386 been excluded from the modelling process because of high collinearity between variables

387 (e,g Canfreq, a finescale variable which was highly correlated with canopy cover measured

388 at the broadscale). Furthermore, finescale models were only included in the best model set

389 (i.e. ΔAICc < 2) for species richness, but combined and broadscale models performed

390 equally well. Variables that described vegetation structural heterogeneity or diversity were

391 only rarely included in the best model sets: SDshrubs was in the best model set for Wren,

392 Tree Pipit and species diversity, although for the latter, the variable was not significant and

393 was of low variable weight (ESM Tables S4 and S5).

394 These results therefore suggest that structural vegetation may be less important for

395 the identification of factors determining species diversity and species distribution in the

396 majority of cases. However, to further our understanding of individual species and bird

397 species diversity, data collection in the field should focus on habitat data which considers

398 horizontal vegetation cover collected at a broad scale, but which includes species-specific

399 estimates of cover of relevant shrub species in the area in order to model distributions of

400 birds in the shrub-forest ecotone. The assessment of horizontal habitat cover can be done

401 quickly and easily by eye from a single location for the whole area of a point count, including

402 cover of easily recognizable shrub species such as Juniper and Rhododendron, whereas

403 detailed structural vegetation measurements (as undertaken here) require considerable

404 effort and access to a much greater area of a given point. The results further suggest that

405 land cover datasets analogous to the data collected here should also be adequate for

406 species distribution modelling in the studied habitat if they are able to estimate the cover of

407 the dominant shrub species. Thus, broadscale habitat data and data on shrub species

408 composition should provide a sufficient basis in identifying relevant species-specific habitat

409 parameters in a mountain environment. Future species distribution models should seek to

410 incorporate species-specific estimates of shrub cover, especially as the dominant species in

411 the area are likely to respond differently to future climate change (Theurillat and Guisan

412 2001; Neuner 2014).

413

414 **Factors affecting bird diversity and distribution at different habitat scales**

415 There was some support that a habitat mosaic was beneficial for some individual species in

416 that Dunnock, Lesser Whitethroat and Wren showed significant non-linear associations with

417 either shrub cover or shrub species frequency in at least one model. Furthermore, shrub

418 cover and frequency occurred in two final models and were positively correlated with bird

419 species diversity (shrub cover) as well as Northern Wheatear presence (shrub frequency).

420 The general overall importance of shrubs can easily be understood as they provide nesting

421 habitat for shrub-nesting species, provide shelter in harsh weather conditions and can shield

422 birds from predators.

423   In addition to overall shrub cover, individual shrub species were also important for

424   some bird species. Bilberry cover was negatively related to bird species diversity,

425   presumably because, in contrast to the other shrub species present, this species does not

426   provide dense cover that could be suitable for nesting. Only Wren was positively associated

427   with Juniper frequency. It was also negatively associated with altitude, which may suggest a

428   link to the different growth characteristics of Juniper along the altitudinal gradient (Hallinger

429   et al. 2010). At high altitudes (>2000m), this shrub species typically grows fairly low to the

430   ground (10-30 cm; Aeschimann et al. 2004), which may make it unsuitable for nesting (due

431   to predation risk for example). Suitable Wren nesting habitat may only be found at lower

432   altitudes (1800 – 2000 m), where Juniper tends to be taller, and possibly less dense.

433   In contrast to Juniper, Rhododendron can still grow up to heights suitable for nesting

434   (30 – 120 cm; Aeschimann et al. 2004) in the upper fringe of the ecotone and could therefore

435   be seen as an attractive alternative for shrub-nesting species. In the combined models,

436   Rhododendron showed a non-linear association with Dunnock presence, which seems to be

437   preferred as a nesting habitat over other shrub species (pers. obs.). In the Alps,

438   Rhododendron can form very large and dense patches on north, west and northwest-facing

439   slopes within the subalpine belt (Pornon and Bernard 1996). Its distribution depends highly

440   on winter snow cover which serves as a protective layer against excessive irradiation and

441   frost (Neuner et al. 1999). However, due to climate change, snow cover is predicted to

442   decrease by the end of the century (Beniston et al. 2003). Taking potential snow

443   accumulation into account, Komac et al. (2016) showed that Rhododendron could

444   experience an important reduction in its realized niche, and that its future habitat could be

445   confined to areas which are today scree and rocky hillside habitats. This outcome suggests

446   that, even if current habitat is maintained, climatic conditions might become less favourable

447   for the persistence of Rhododendron and that suitable habitat for shrub-nesting species in

448   the forest-shrub ecotone will disappear.

449

450   **Conservation implications**

451 The loss of open habitats due to abandonment of grazing (Gehrig-Fasel et al. 2007; Roura-

452 Pascual et al. 2004; MacDonald et al. 2000) and climate change (Lenoir et al. 2008; Pauli et

453 al. 2007) is likely to continue in the future to the extent that significant areas of more open

454 habitats, including the shrub-grassland ecotone, will be replaced by forest. To maintain

455 ecotone habitat, it may therefore be necessary to counteract shrub and indeed forest

456 encroachment in targeted areas in order to keep a heterogeneous character of the forest-

457 shrub ecotone. Possible methods to counteract shrub-encroached areas could be

458 mechanical shrub clearance or the re-establishment of grazing (e.g rotational grazing

459 systems with appropriate stocking level; Probo et al. 2014). However, mechanical shrub

460 clearance can only be applied if the required equipment can be transported to the

461 encroached areas, but accessibility by road is often limited in mountain areas. Moreover,

462 encroached areas are frequently characterized by a steep terrain, which influences the

463 effectiveness of traditional grazing practices, as livestock tends to concentrate in flat areas

464 and avoids steep slopes (Bailey et al. 1996, Mueggler 1965). Therefore, more specific

465 pastoral practices involving targeted grazing are needed. The strategic placement of mineral

466 mix supplements (MMS) would be one viable management option to be used in rugged

467 shrub-encroached locations (Pittarello et al. 2015). The placement of MMS would lead to

468 increased trampling in the surrounding 100 m of MMS site and therefore would reduce shrub

469 cover (Probo et al. 2013). A further more targeted option is the use of temporary night camp

470 areas (TNCA), where cows are fenced for up to two nights in shrub-encroached areas.

471 Through intense trampling within the fenced area, shrubs get mechanically damaged and

472 subsequently decrease in cover (Tocco et al. 2013; Pittarello et al. 2016, Probo et al. 2016).

473 In the long-term, this pastoral technique has the additional advantage that it increases plant

474 diversity (Pittarello et al. 2016), which in turn might positively influence invertebrate

475 availability (Tocco et al. 2013) for birds. Any such initiatives would have to be managed

476 carefully so as to open-up encroached areas whilst maintaining a reasonable level of shrub

477 cover. Similarly, grazing also has the potential to maintain open areas above the ecotone,

478 which is important for Northern Wheatear and Water Pipit which both are open habitat

479   species at high altitudes. Although, grazing could represent a viable management option in

480   forest-ecotone areas, it is still unknown which potential direct or indirect effects it can have

481   on different bird species groups (e.g. grassland, ecotone, forest) as it is likely that some

482   species might be more affected than others. Moreover, grazing management targeted in the

483   wrong areas, or applied at intensive levels, could also be detrimental to biodiversity.

484   It should be noted that habitat requirements among the most common bird species

485   within the forest-shrub ecotone can differ considerably. Chamberlain et al. (2013) argued

486   that management for the maintenance of high altitude grassland would be preferable to

487   allowing forest expansion due to the high proportion of specialist species and species of

488   conservation concern that could be negatively impacted. However, our data showed that

489   forested areas with high shrub cover had the highest bird diversity. Nevertheless, the

490   ecotone holds important bird species that were not well covered by our methods (von dem

491   Bussche et al. 2008; Braunisch et al. 2016), and also has a high biodiversity of other taxa

492   (Dirnböck et al. 2011). In order to meet a range of species-specific habitat requirements, it

493   might therefore be important to sustain a high level of heterogeneity and to maintain a

494   habitat mosaic within the ecotone (Patthey et al. 2012). Management recommendations

495   need to be adopted for areas differing in altitude, topography, shrub species composition

496   and the degree of shrub encroachment at appropriate scales (Braunisch et al. 2016).

497   Depending on the targeted area, it might therefore be necessary to apply a combination of

498   different management techniques and to adjust the time period of application to promote

499   heterogeneity. There is the possibility of managing for diverse landscapes that can

500   incorporate a range of needs for different habitat types which facilitates species resilience

501   and resistance to environmental change (e.g. Brambilla et al. 2017), but further work is

502   needed on the most appropriate scale of management by which this can be achieved.

503

504

505

506

507

508

509

510

511

512

513 **References**

514 Aeschimann D, Lauber K, Moser, DM, Theurillat JD (2004) Flora alpina. Zanichelli, Bologna

515 Arlettaz R, Patthey P, Baltic M, Leu T, Schaub M, Palme R, Jenni-Eiermann S.(2007)

516   Spreading free-riding snow sports represent a novel serious threat for wildlife. Proc R

517   Soc B Biol Sci 267:1219-1224

518 Bartoń K (2013) MuMIn: Multi-model inference. R package version 1.9.0 ed

519 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using

520   lme4. J Stat Softw 67:1-48

521 Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996)

522   Mechanisms that result in large herbivore grazing distribution patterns. J Range Manage

523   49: 386-400

524 Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) Bird Census Techniques, 2nd edn.

525   Academic, London

526 Beniston M, Keller F, Koffi B, Goyette S (2003) Estimates of snow accumulation and volume

527   in the Swiss Alps under changing climatic conditions. Theoret Appl Climatol 76:125-140

528 Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the

529   key? Trends Ecol Evol, 18: 82-188

530 Böhm R, Auer I, Brunetti M, Maugeri M, Nanni T, Schöner W (2001) Regional temperature

531   variability in the European Alps; 1769-1998 from homogenized instrumental time series.

532   Int J Climatol 21:1779-1801

533 Brambilla M, Pedrini P, Rolando A, Chamberlain DE (2016) Climate change will increase the

534 potential conflict between skiing and high-elevation bird species in the Alps. J Biogeogr

535 43:2299–2309

536 Brambilla M, Caprio E, Assandri G, Scridel D, Bassi E, Bionda R, Celada C, Falco R,

537 Bogliani G, Pedrini P, Rolando A, & Chamberlain D (2017) A spatially explicit definition

538 of conservation priorities according to population resistance and resilience, species

539 importance and level of threat in a changing climate. Divers Distrib in press

540 Braunisch V, Patthey P, Arlettaz R (2016) Where to Combat Shrub Encroachment in Alpine

541 Timberline Ecosystems: Combining Remotely-Sensed Vegetation Information with

542 Species Habitat Modelling. PLoS One 11(10):e0164318

543 Burnham KP, Anderson DR (2002) Model selection and multimodel inference - a practical

544 information-theoretic approach, 2nd edn. Springer, New York

545 von dem Bussche F, Spaar R, Schmid H, Schröder B (2008) Modelling the recent and

546 potential future spatial distribution of the Ring Ouzel (*Turdus torquatus*) and Blackbird

547 (*T. merula*) in Switzerland. J Orn 149:529-544

548 Cannone N, Sgorbati S, Guglielmin M (2007) Unexpected impacts of climate change on

549 alpine vegetation. Front Ecol Environ 5:360-364

550 Chamberlain DE, Brambilla M, Pedrini P, Caprio E, Rolando A (2016) Alpine bird

551 distributions along elevation gradients: the consistency of climate and habitat effects

552 across geographic regions. Oecologia 181:1139-1150

553 Chamberlain DE, Negro M, Caprio E, Rolando A (2013) Assessing the sensitivity of alpine

554 birds to potential future changes in habitat and climate to inform management

555 strategies. Biol Conserv, 167:127-135

556 Dirnböck T, Essl F, Babitsch W (2011) Disproportional risk for habitat loss of high altitude

557 endemic species under climate change. Glob Change Biol 17:990-996

558 Freemark KE, Merriam HG (1986) Importance of area and habitat heterogeneity to bird

559 assemblages in temperate forest fragments. Biol Conserv 36:115-141

560 Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and

561   winter snow cover promote shrub expansion into alpine tundra in Scandinavia. New

562   Phytol 186:890-899

563 Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global

564   meta-analysis of treeline response to climate warming. Ecol Lett 12:1040-1049

565 Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps:

566   Climate change or land abandonment? J Veg Sci 18:571:582

567 Guerta RS, R. Cintra R (2014) Effects of habitat structure on the spatial distribution of two

568   species of Tinamous (Aves: Tinamidae) in a Amazon terra-firme forest. Ornitol Neotrop

569   25(1):73-86.

570 Hovick TJ, Elmore RD, Fuhlendorf SD (2014) Structural heterogeneity increases diversity of

571   non-breeding grassland birds. Ecosphere 5(5):62

572 Kapos VJ, Rhind J, Edwards M, Price MF, Ravilious C (2000) Developing a map of the

573   world's mountain forests. In: Forests in Sustainable Mountain Development: A State-of-

574   Knowledge Report for 2000, M.F. Price and N. Butt (eds.), CAB International,

575   Wallingford: 4–9.

576 Komac B, Esteban P, Trapero L, Caritg R (2016) Modelization of the Current and Future

577   Habitat Suitability of Rhododendron ferrugineum Using Potential Snow Accumulation.

578   PLoS One 11(1):e0147324

579 Körner C, Ohsawa M (2006) Mountain systems. In: Hassan R, Scholes R, Ash N (eds)

580   Ecosystem and human well-being: current state and trends. Millennium Ecosystem

581   Assessment, Island Press, Washington 1: 681-716.

582 Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral abandonment

583   for the structure and diversity of the alpine avifauna. J Appl Ecol 41:294-304

584 Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A Significant Upward Shift

585   in Plant Species Optimum Elevation During the 20th Century. Science 320(5884):1768-

586   1771

587 MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42:594-598

588   MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J,

589   Gibon A (2000) Agricultural abandonment in mountain areas of Europe: Environmental

590   consequences and policy response. J Environ Manage 59:47-69

591   Moran PAP (1950) Notes on continuous stochastic phenomena. Biometrika 37:17-23

592   Mueggler WF (1965) Cattle distribution on steep slopes. J Range Manage 18: 255-257

593   Neuner G (2014) Frost resistance in alpine woody plants. Front Plant Sci 5:654

594   Neuner G, Ambach D, Aichner K (1999) Impact of snow cover on photoinhibition and winter

595   desiccation in evergreen Rhododendron ferrugineum leaves during subalpine winter.

596   Tree Physiol 19:725-732

597   Patthey P, Signorell N, Rotelli L, Arlettaz R (2012) Vegetation structural and compositional

598   heterogeneity as a key feature in Alpine black grouse microhabitat selection:

599   conservation management implications. Eur J Wildl Res 58:59-70

600   Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr G (2007) Signals of range expansion and

601   contractions of vascular plants in the high Alps: observations (1994-2004) at the

602   GLORIA master site Schrankogel, Tyrol, Austria. Glob Change Biol 13:147-156

603   Pittarello M, Probo M, Lonati M, Bailey DW, Lombardi G (2015) Effects of traditional salt

604   placement and strategically placed mineral mix supplements on cattle distribution in the

605   Western Italian Alps. Grass Forage Sci 71(4):529-539.

606   Pittarello M, Probo M, Lonati M, Lombardi G (2016) Restoration of sub-alpine shrub-

607   encroached grasslands through pastoral practices: effects on vegetation structure and

608   botanical composition. Appl Veg Sci 19(3):381-390

609   Probo M, Pittarello M, Lonati M, Lombardi G (2016) Targeted grazing for the restoration of

610   sub-alpine shrub-encroached grasslands. Ital J Agron 11(4):268-272

611   Pornon A, Doche B (1996) Age structure and dynamics of Rhododendron ferrugineum L.

612   populations in the northwestern French Alps. J Veg Sci 7:265-272

613   Probo M, Lonati M, Pittarello M, Bailey DW, Garbarino M, Gorlier A, Lombardi G (2014)

614   Implementation of a rotational grazing system with large paddocks changes the

615   distribution of grazing cattle in the south-western Italian Alps. Rangeland J 36:445–458

616 Probo M, Massolo A, Lonati M, Bailey DW, Gorlier A, Maurino L, Lombardi G (2013) Use of

617   mineral mix supplements to modify the grazing patterns by cattle for the restoration of

618   sub-alpine and alpine shrub-encroached grasslands. Rangeland J 35:85–93

619 R Development Core Team (2016) R: A Language and Environment for Statistical

620   Computing. R Foundation for Statistical Computing, Vienna

621 Rolando A, Caprio E, Rinaldi E, Ellena, I (2007) The impact of high-altitude ski-runs on

622   alpine grassland bird communities. J Appl Ecol 44:210-219

623 Roura-Pascual N, Pons P, Etienne M, Lambert B (2005) Transformation of a Rural

624   Landscape in the Eastern Pyrenees Between 1953 and 2000. Mt Res Dev 25(3):252-

625   261

626 Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2008) Climate change, elevational range

627   shifts and bird extinctions. Conserv Biol 22:140-150

628 Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the

629   European Alps: A review. Clim Change 50:77-109

630 Tocco C, Probo M, Lonati M, Lombardi G, Negro M, Nervo B, Rolando A, Palestrini C (2013)

631   Pastoral practices to reverse shrub encroachment of sub-alpine grasslands: dung

632   beetles (Coleoptera, Scarabaeoidea) respond more quickly than vegetation. PLoS One

633   8(12):e83344

634 Viterbi R, Cerrato C, Bassano B, Bionda R, von Hardenberg A, Provenzale A, Bogliani G

635   (2013) Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach.

636   Community Ecol. 14:18-30

637 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and

638   Extensions in Ecology with R, 1st edn. Springer, New York

639

640

641 **Table 1** Variables considered in the analysis, and the scale at which they were measured.

642 The broadscale category was measured at the whole point count location scale and

643 finescale category was measured at the plot level (n = 11 for each point)

644

Parameter	Category	Description
Canopy	Broadscale	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Shrubs	Broadscale	Percentage cover of shrubs within a radius of 100 m of the point count centre
Trees	Broadscale	Number of mature (greater than c. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Rocks	Broadscale	Percentage cover of rocks within a radius of 100 m of the point count centre
HCOV	Broadscale	Shannon Index of broadscale habitat diversity (H' = − $\sum p_i \ln p_i$, where p_i is the percentage cover of the different habitat types)
Alt	Broadscale	Altitude of the point count location in meters asl. estimated from a GPS
H1	Finescale	Shannon Index of vegetation density diversity at 1 m above the ground
H05	Finescale	Shannon Index of vegetation density diversity at 0,5 m
SDShrub	Finescale	Shrub height heterogeneity measured as the standard deviation of the average shrub height at the point count location
Canfreq	Finescale	Frequency of vegetation sampling points for a point count location where canopy was present
Shrubfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs were present
Rodfreq	Finescale	Proportion of vegetation sampling points for a point count location where Rhododendron was the dominant shrub species
Junfreq	Finescale	Frequency of vegetation sampling points for a point count location where Juniper was the dominant shrub species
Bilfreq	Finescale	Frequency of vegetation sampling points for a point count location where bilberry was the dominant shrub species

645

646   **Table 2** Final significant model-averaged parameters of the model set derived by combining

647   significant model-averaged parameters of broadscale and finescale habitat structure model

648   sets for bird diversity, richness and the commonest species in the study area. The scale (B =

649   broadscale, F= finescale), estimate, standard error (SE), test value (z) and p value are given

650   for each parameter. Full details for all species and parameters are given in Table S4

651

Dependent Variable	Parameter	Scale	Estimate ± SE	z	p
Lesser Whitethroat	Shrubs	B	2.171 ± 0.729	2.930	0.003
	Shrubs²	B	-2.041 ± 0.823	2.439	0.015
Tree Pipit	Rock	B	-1.416 ± 0.648	2.151	0.032
	SDshrub	F	1.438 ± 0.514	2.754	0.006
	Rodfreq	F	-1.120 ± 0.480	2.296	0.022
Dunnock	Trees	B	-0.939 ± 0.471	1.963	0.050
	Rodfreq	F	1.601 ± 0.672	2.351	0.019
	Rodfreq²	F	-1.363 ± 0.589	2.286	0.022
Northern Wheatear	Alt	B	2.872 ± 0.482	5.873	≤ 0.000
	Shrubfreq	F	-2.325 ± 0.469	4.884	≤ 0.000
	Shrubfreq²	F	-0.618 ± 0.031	19.595	≤ 0.000
Wren	Alt	B	-2.435 ± 0.875	2.747	0.006
	Junfreq²	F	0.583 ± 0.291	1.974	0.048
	SDshrub	F	1.096 ± 0.549	1.969	0.049
Chaffinch	Alt	B	-1.533 ± 0.409	3.687	≤ 0.000
	Canfreq	F	1.238 ± 0.404	3.016	0.003
Species richness	Canfreq	F	0.169 ± 0.059	2.838	0.005
Species diversity	Shrubs	B	0.221 ± 0.062	3.508	≤ 0.000
	Canfreq	F	0.131 ± 0.053	2.451	0.014
	Bilfreq	F	-0.171 ± 0.056	2.990	0.003
	Bilfreq²	F	-0.063 ± 0.025	2.491	0.013

652

653

654 **Table 3** Variables with the highest importance (Akaike weight > 0.70) for combined models,

655 derived from all combinations of models for each dependent variable, grouped according to

656 whether they were broad- or finescale. Full details are given in ESM Table S5. A dash

657 indicates Akaike weight < 0.70 for a given scale. Variable codes are given in Table 1 and

658 Table S1

659

Variable	Broadscale	Finescale
Tree Pipit	Rock, Shrubs^2	SDShrub, Rodfreq
Water Pipit	Alt	Canfreq
Dunnock	Trees	Rodfreq, Rodfreq^2
Northern Wheatear	Alt	Shrubfreq
Lesser Whitethroat	Shrubs, Shrubs²	-
Wren	Alt, Shrubs	SDShrub,Junfreq²
Chaffinch	Alt	Canfreq
Species richness	-	Canfreq
Species diversity	Shrubs	-

660

Figure legends

Fig. 1

Relationship between shrub cover (%) and bird species diversity based on the combined model. Black circles represent the H-value in relation to shrub cover for a given point count, where the size of the circle is proportional to the number of points for a given H-value at a particular level of shrub cover

Fig. 2

Relationship between shrub species frequency (Rhododendron, Juniper, bilberry) and the probability of occurrence for individual bird species (Dunnock, Tree Pipit, Wren) and bird species diversity based on combined models. Black circles represent the point counts where a species was present/absent in relation to shrub species frequency, and the size of the circle is proportional to the number of points for a given category of presence/absence at a particular level of shrub frequency. For bird species diversity, black circles represent the H-value in relation to bilberry frequency, where the size of the circle is again proportional to the number of points for a given H-value at a particular level of bilberry frequency.

Fig. 3 The ten best ranked models according to AICc (where smaller AICc values indicate better performing models) for individual species, and for species richness and diversity. Each model is classified according to whether variables were finescale (white bars), broadscale (black bars) or a combination of the two (grey bars) in each model. The dashed horizontal line indicates ΔAICc = 2 (i.e. models below the line are considered to be in the best model set)

Fig. 1

Bird species diversity

686
687
688
689
690
691
692
693
694
695
696
697
698
699
700

701
702
703
704
705
706
707
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724

Fig. 2

Bird species diversity

Wren

Dunnock

Tree Pipit
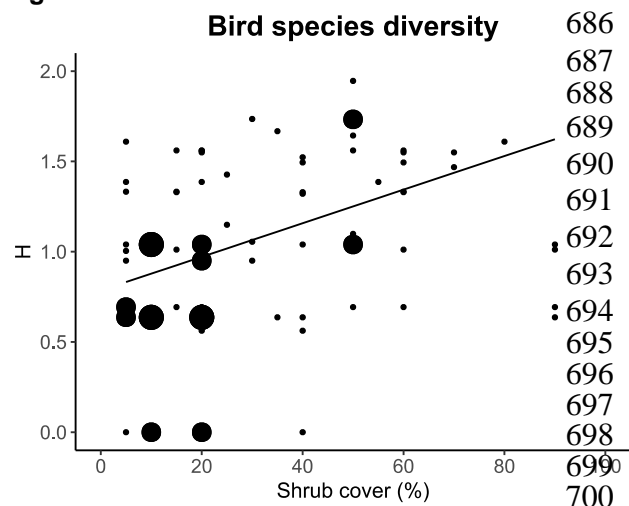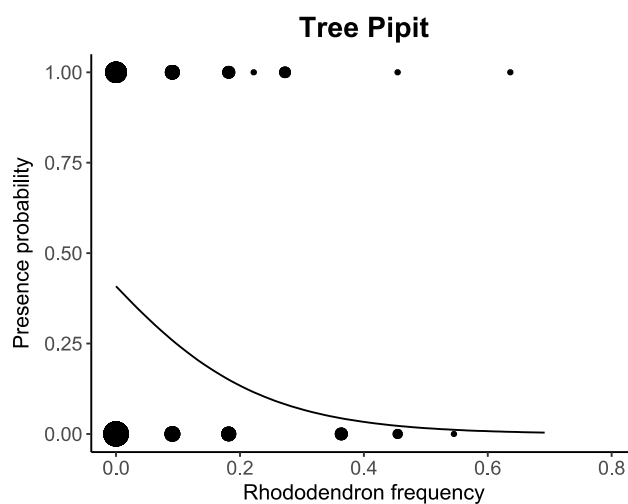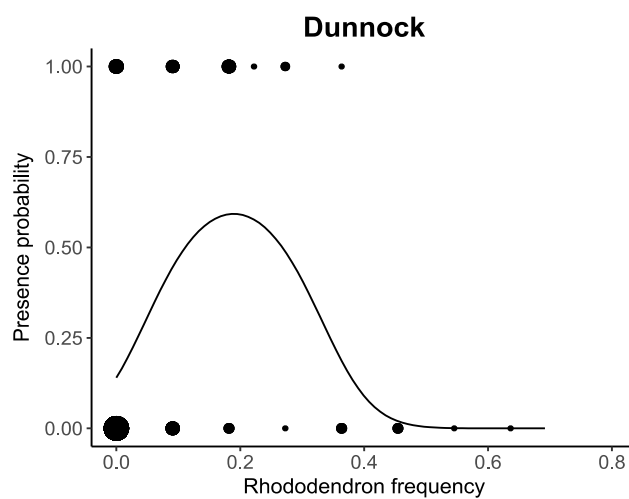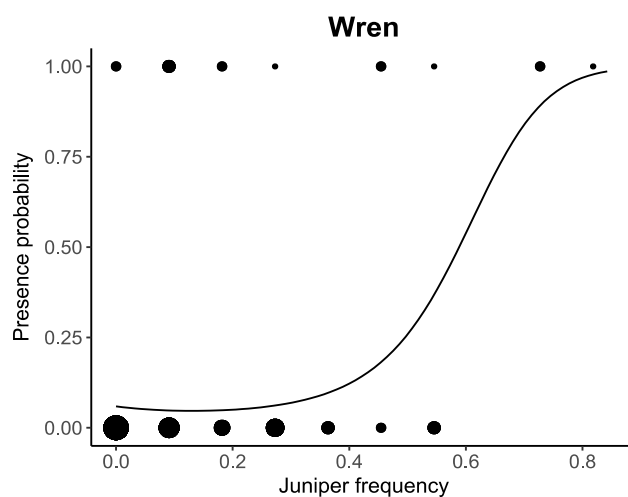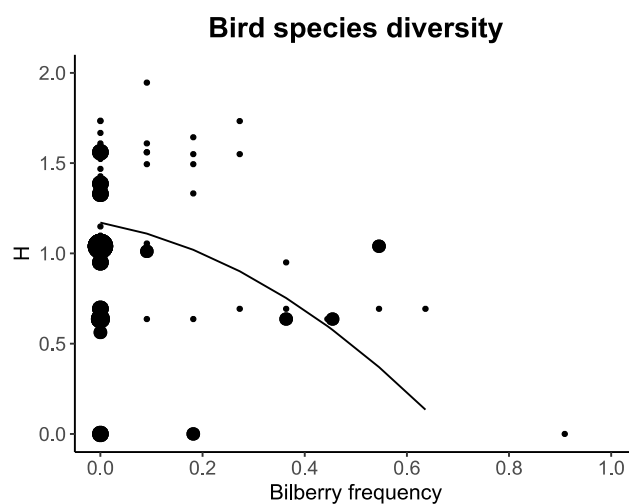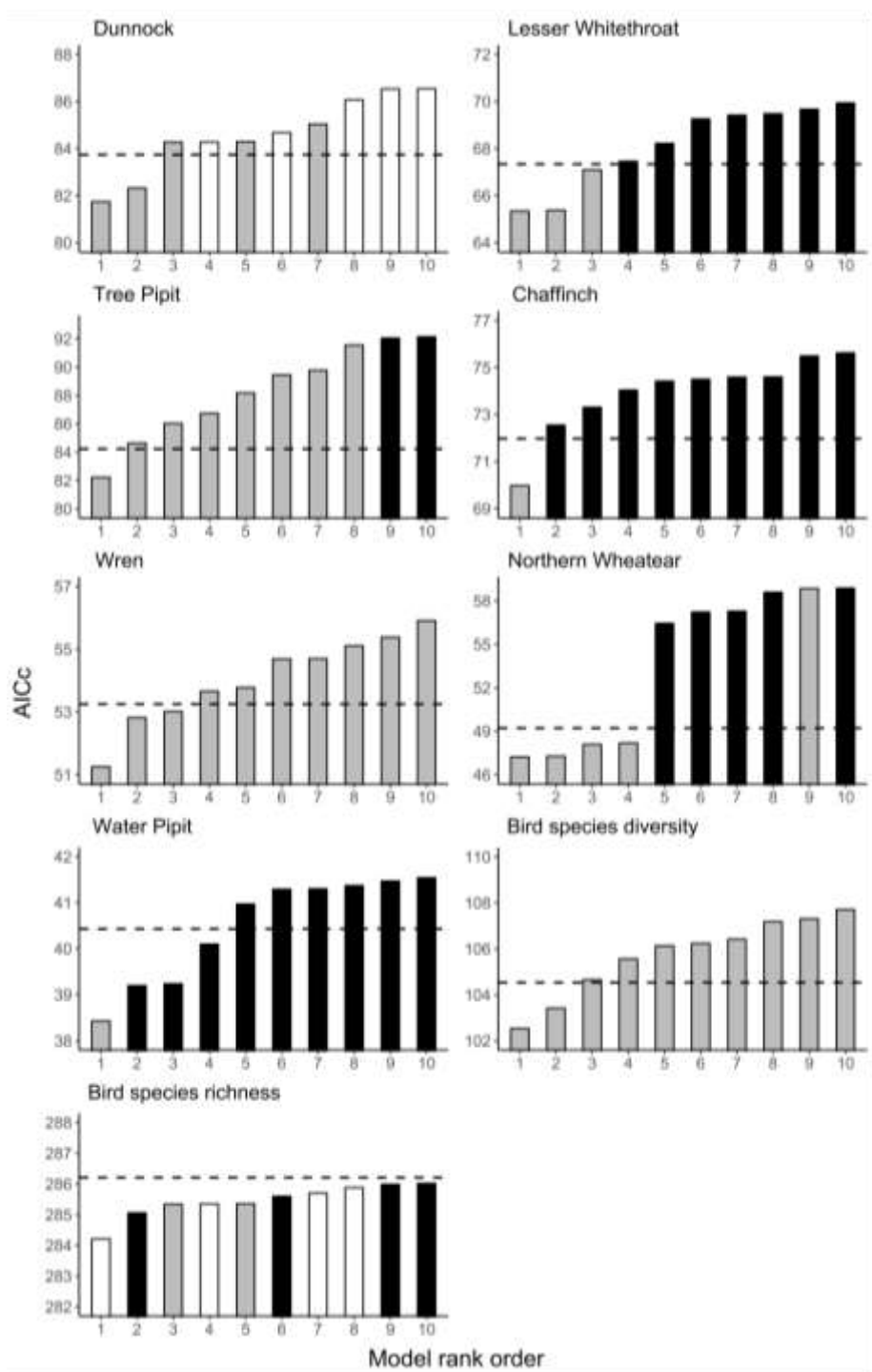
727 **Electronic Supplementary Material – Journal of Ornithology**

728

729 **The contribution of broadscale and finescale habitat structure to the distribution and**

730 **diversity of birds in an Alpine forest-shrub ecotone**

731 Susanne Jähnig[1]*, Riccardo Alba[1], Cristina Vallino[1], Domenico Rosselli[2], Marco Pittarello[3],

732 Antonio Rolando[1] & Dan Chamberlain[1]

733

734 [1] Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13,
735 10123, Turin, Italy.
736 [2] Ente di Gestione delle Aree Protette delle Alpi Cozie, Via Fransuà Fontan 1, 10050 Salbertrand,
737 Italy.
738 [3] Department of Agricultural, Forest and Food Sciences, University of Turin, Largo Paolo Braccini
739 2 ,10095 Grugliasco, Italy.

740

741 *Corresponding author

742 Email: susanne.jaehnig@gmail.com

743

744

745

746

747

748

749

750

751

752

753

754

755 **Table S1** Variables which were removed after VIF and correlation coefficient calculations, or

756 during the model reduction process. The broadscale category was measured at the whole

757 point count location scale and finescale category was measured at the plot level (n = 11 for

758 each point)

Parameter	Category	Description
Grass	Broadscale	Percentage cover of grass within a radius of 100 m of the point count centre
H0	Finescale	Shannon-Index of vegetation density diversity at ground level
Altgrs	Finescale	Average grass height across the plots at each point count location
Altshrub	Finescale	Average shrub height across the plots at each point count location
SDgrs	Finescale	Standard deviation of the average grass height at the point count location
Othfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs different from Juniper, Rhododendron and bilberry were the dominant shrub species

759

760

761 **Table S2** Model-averaged estimates of the model set for broadscale habitat structure

762 presented for bird diversity, richness and the commonest species in the study area. The

763 estimate, standard error (SE), test value (z) and p value are given for each parameter

764

Dependent Variable	Parameter	Estimate ± SE	z	p
Tree Pipit	Alt	-0.559 ± 0.355	1.552	0.121
	Trees	0.247 ± 0.308	0.790	0.429
	Shrubs	0.292 ± 0.497	0.583	0.560
	Shrubs²	0.905 ± 0.480	1.857	0.063
	Rock	-1.403 ± 0.616	2.243	0.025
	HCOV	0.445 ± 0.420	1.047	0.295
Water Pipit	Alt	2.095 ± 1.014	2.036	0.042
	Trees	-18.384 ± 16.692	1.085	0.278
	Shrubs	-0.851 ± 0.777	1.081	0.280
	Shrubs²	-0.418 ± 0.849	0.485	0.627
	Rock	0.185 ± 0.769	0.238	0.812
	HCOV	-0.714 ± 0.661	1.065	0.287
Dunnock	Alt	0.547 ± 0.468	1.154	0.249
	Trees	-1.136 ± 0.511	2.191	0.028
	Shrubs	1.029 ± 0.466	2.183	0.029
	Shrubs²	-0.335 ± 0.387	0.857	0.391
	Rock	-0.693 ± 0.527	1.298	0.194
	HCOV	0.585 ± 0.423	1.365	0.172
Northern Wheatear	Alt	1.907 ± 0.789	2.384	0.017
	Trees	-2.382 ± 1.658	1.418	0.156
	Shrubs	-1.661 ± 1.020	1.613	0.107
	Shrubs²	-0.453 ± 0.988	0.452	0.651
	Rock	-0.774 ± 0.768	0.997	0.319
	HCOV	1.071 ± 0.908	1.168	0.243
Lesser Whitethroat	Alt	0.331 ± 0.496	0.658	0.511
	Trees	-0.257 ± 0.397	0.639	0.523
	Shrubs	1.914 ± 0.757	2.492	0.013
	Shrubs²	-1.758 ± 0.834	2.075	0.038
	Rock	0.048 ± 0.480	0.098	0.922
	HCOV	0.731 ± 0.550	1.313	0.189
Wren	Alt	-2.263 ± 0.663	3.358	0.001
	Trees	0.015 ± 0.385	0.039	0.969
	Shrubs	2.204 ± 0.897	2.421	0.015
	Shrubs²	-1.351 ± 0.630	2.109	0.035

	Rock	-0.080 ± 0.784	0.100	0.920
	HCOV	0.208 ± 0.649	0.317	0.751
Chaffinch	Alt	-1.638 ± 0.509	3.177	0.001
	Trees	1.141 ± 0.497	2.261	0.024
	Shrubs	0.458 ± 0.399	1.129	0.259
	Shrubs²	0.181 ± 0.338	0.530	0.596
	Rock	-0.234 ± 0.474	0.486	0.627
	HCOV	0.561 ± 0.467	1.185	0.236
Rock Bunting	Alt	-0.388 ± 0.419	0.912	0.362
	Trees	0.380 ± 0.353	1.062	0.288
	Shrubs	0.672 ± 0.492	1.348	0.178
	Shrubs²	-0.152 ± 0.378	0.398	0.690
	Rock	0.746 ± 0.376	1.955	0.051
	HCOV	0.376 ± 0.376	0.987	0.324
Species diversity	Alt	-0.125 ± 0.053	2.320	0.020
	Trees	0.139 ± 0.054	2.524	0.012
	Shrubs	0.221 ± 0.081	2.706	0.007
	Shrubs²	-0.116 ± 0.049	2.317	0.021
	Rock	-0.044 ± 0.060	0.721	0.471
	HCOV	0.084 ± 0.063	1.319	0.187
Species richness	Alt	-0.097 ± 0.082	1.170	0.242
	Trees	0.134 ± 0.064	2.066	0.039
	Shrubs	0.180 ± 0.095	1.876	0.061
	Shrubs²	-0.103 ± 0.075	1.359	0.174
	Rock	-0.023 ± 0.079	0.282	0.778
	HCOV	0.057 ± 0.090	0.621	0.535

765

766

767 **Table S3** Model-averaged parameters of the model set for finescale habitat structure

768 presented for bird diversity, richness and the commonest species in the study area. The

769 estimate, standard error (SE), test value (z/t) and p value are given for each parameter

770

Dependent Variable	Parameter	Estimate ± SE	z / t	p
Lesser Whitethroat	SDshrub	0.144 ± 0.296	0.477	0.633
	Bilfreq	-0.375 ± 0.681	0.543	0.587
	Bilfreq²	-1.364 ± 1.199	1.119	0.263
	H05	0.251 ± 0.256	0.966	0.334
	H1	0.290 ± 0.272	1.047	0.295
	Canfreq	0.069 ± 0.318	0.214	0.831
Tree Pipit	SDshrub	1.564 ± 0.534	2.889	0.004
	Rodfreq	-1.007 ± 0.544	1.827	0.068
	Rodfreq²	0.167 ± 0.278	0.593	0.553
	H05	0.481 ± 0.387	1.223	0.221
	H1	0.415 ± 0.344	1.187	0.235
	Canfreq	0.090 ± 0.315	0.280	0.779
Dunnock	SDshrub	-0.614 ± 0.497	1.215	0.224
	Rodfreq	2.036 ± 0.670	2.995	0.003
	Rodfreq²	-1.665 ± 0.551	2.974	0.003
	H05	0.086 ± 0.309	0.275	0.783
	H1	0.002 ± 0.377	0.006	0.995
	Canfreq	-0.181 ± 0.356	0.501	0.617
Rock Bunting	SDshrub	-0.220 ± 0.447	0.486	0.627
	Shrubfreq	-0.270 ± 0.357	0.746	0.456
	Shrubfreq²	-0.300 ± 0.357	0.827	0.408
	H05	-0.063 ± 0.335	0.184	0.854
	H1	-0.168 ± 0.364	0.453	0.650
	Canfreq	0.442 ± 0.328	1.328	0.184
Northern Wheatear	SDshrub	-0.925 ± 0.727	1.253	0.210
	Shrubfreq	-0.646 ± 0.570	1.115	0.265
	Shrubfreq²	-1.077 ± 0.491	2.157	0.031
	H05	0.254 ± 0.403	0.620	0.535
	H1	0.075 ± 0.669	0.110	0.912
	Canfreq	-2.454 ± 0.932	2.592	0.010
Wren	SDshrub	0.970 ± 0.416	2.329	0.020
	Junfreq	0.113 ± 0.565	0.198	0.843
	Junfreq²	0.502 ± 0.236	2.128	0.033
	H05	-0.012 ± 0.351	0.032	0.974

	H1	0.252 ± 0.312	0.795	0.427
	Canfreq	0.205 ± 0.401	0.505	0.614
Chaffinch	SDshrub	-0.027 ± 0.389	0.070	0.945
	Shrubfreq	-0.462 ± 0.328	1.389	0.165
	Shrubfreq²	0.328 ± 0.313	1.031	0.303
	H05	-0.337 ± 0.313	1.061	0.289
	H1	-0.279 ± 0.384	0.716	0.474
	Canfreq	1.738 ± 0.444	3.855	≤ 0.000
Water Pipit	SDshrub	0.340 ± 0.676	0.582	0.561
	Bilfreq	0.600 ± 0.466	1.270	0.204
	Bilfreq²	0.020 ± 0.250	0.079	0.937
	H05	1.105 ± 3288.174	0.000	1.000
	H1	11.995 ± 2901.247	0.004	0.997
	Canfreq	-51.512 ± 8599.602	0.006	0.995
Species diversity	SDshrub	0.110 ± 0.064	1.699	0.089
	Bilfreq	-0.100 ± 0.065	1.526	0.127
	Bilfreq²	-0.054 ± 0.023	2.350	0.019
	H05	-0.094 ± 0.052	1.769	0.078
	H1	0.040 ± 0.062	0.642	0.521
	Canfreq	0.178 ± 0.053	3.293	0.001
Species richness	SDshrub	0.068 ± 0.071	0.945	0.345
	Bilfreq	-0.057 ± 0.116	0.483	0.629
	Bilfreq²	-0.073 ± 0.050	1.444	0.149
	H05	-0.065 ± 0.069	0.936	0.349
	H1	0.024 ± 0.068	0.358	0.721
	Canfreq	0.153 ± 0.064	2.349	0.019

771

772

773 **Table S4** Final model-averaged parameters of the model set derived by combining

774 significant model-averaged parameters of broadscale and finescale habitat structure, and

775 top model sets for bird diversity, richness and the commonest species in the study area. The

776 scale (B = broadscale, F= finescale), estimate, standard error (SE), test value (z) and p

777 value are given for each parameter

778

Dependent Variable	Parameter	Scale	Estimate ± SE	z	p
Lesser Whitethroat	Shrubs	B	2.171 ± 0.729	2.930	0.003
	Shrubs²	B	-2.041 ± 0.823	2.439	0.015
	Bilfreq	F	-0.893 ± 0.685	1.284	0.199
	Bilfreq²	F	-0.926 ± 0.960	0.949	0.343
Tree Pipit	Rock	B	-1.416 ± 0.648	2.151	0.032
	SDshrub	F	1.438 ± 0.514	2.754	0.006
	Shrubs	B	0.222 ± 0.457	0.478	0.632
	Shrubs²	B	0.748 ± 0.427	1.721	0.085
	Rodfreq	F	-1.120 ± 0.480	2.296	0.022
Dunnock	Trees	B	-0.939 ± 0.471	1.963	0.050
	Shrubs	B	0.808 ± 0.485	1.646	0.010
	Rodfreq	F	1.601 ± 0.672	2.351	0.019
	Rodfreq²	F	-1.363 ± 0.589	2.286	0.022
Northern Wheatear	Alt	B	2.872 ± 0.482	5.873	≤ 0.000
	Shrubfreq	F	-2.325 ± 0.469	4.884	≤ 0.000
	Shrubfreq²	F	-0.618 ± 0.031	19.595	≤ 0.000
	Canfreq	F	-1.239 ± 0.700	1.742	0.082
Wren	Alt	B	-2.435 ± 0.875	2.747	0.006
	SDshrub	F	1.096 ± 0.549	1.969	0.049
	Shrubs	B	1.649 ± 0.923	1.765	0.078
	Shrubs²	B	-1.095 ± 0.712	1.516	0.129
	Junfreq	F	0.306 ± 0.761	0.399	0.690
	Junfreq²	F	0.583 ± 0.291	1.974	0.048
Chaffinch	Alt	B	-1.533 ± 0.409	3.687	≤ 0.000
	Canfreq	F	1.238 ± 0.404	3.016	0.003
Water Pipit	Alt	B	1.926 ± 0.985	1.925	0.054
	Canfreq	F	-48.267 ± 14751.960	0.003	0.997
Species richness	Shrubs	B	0.095 ± 0.063	1.481	0.139
	Canfreq	F	0.169 ± 0.059	2.838	0.005
Species diversity	Alt	B	-0.065 ± 0.062	1.039	0.299

SDshrub	F	0.066 ± 0.060	1.090	0.276
H05	F	-0.081 ± 0.048	1.657	0.097
Shrubs	B	0.221 ± 0.062	3.508	≤ 0.000
Shrubs²	B	-0.083 ± 0.047	1.739	0.082
Canfreq	F	0.131 ± 0.053	2.451	0.014
Bilfreq	F	-0.171 ± 0.056	2.990	0.003
Bilfreq²	F	-0.063 ± 0.025	2.491	0.013

779

780

781

782

783

784

785

786

787

788

789

790

791

792

793

794

795

796 **Table S5** Variables weights across all combinations of models, considering either

797 broadscale, finescale or combined models. Weights were calculated based on Akaike

798 weights for each model, which is expressed as the likelihood contribution of each model as a

799 proportion of the summed likelihood contributions of all models. The weight for each variable

800 is the sum of model weights for all models in which a given variable was present (Burnham &

801 Anderson 2002). Output is shown only if a given model type was amongst the top model set

802 (i.e. ΔAICc < 2). For example, no broadscale or finescale models were in the best model set

803 for Dunnock (see Fig. 3), hence variable weights are presented only for combined models. A

804 missing value indicates that a variable was not included in the model averaging procedure

805 for that particular species/scale. Variables are defined in Table 1 and Table S3

806 (a) Broadscale

Variable	Alt	HCOV	Rock	Shrubs	Shrubs^2	Trees
Water Pipit	0.92	0.40	0.28	0.45	0.29	0.90
Species richness	0.42	0.33	0.26	0.78	0.52	0.71

807

808 (b) Finescale

Variable	Canfreq	H05	H1	Bilfreq	Bilfreq^2	SDshrub
Species richness	0.82	0.34	0.26	0.35	0.57	0.35

809

810

811   (c) Combined

Variable	Broadscale					Finescale										
	Alt	Rock	Shrubs	Shrubs^2	Trees	Shrubfreq	Shrubfreq²	H05	Canfreq	Junfreq	Junfreq²	Rodfreq	Rodfreq^2	SDshrub	Bilfreq	Bilfreq²
Tree Pipit	-	0.97	0.26	0.84	-	-	-	-	-	-	-	0.94	-	0.99	-	-
Lesser Whitethroat	-	-	1.00	1.00	-	-	-	-	-	-	-	-	-	-	0.51	0.52
Dunnock	-	-	0.60	-	0.80	-	-	-	-	-	-	0.86	0.97	-	-	-
Northern Wheatear	1.00	-	-	-	-	1.0	0.39	-	0.50	-	-	-	-	-	-	-
Wren	1.00	-	0.74	0.63	-	-	-	-	-	0.34	0.82	-	-	0.88	-	-
Water Pipit	0.98	-	-	-	-	-	-	-	0.97	-	-	-	-	-	-	-
Chaffinch	1.00	-	-	-	-	-	-	-	0.99	-	-	-	-	-	-	-
Species diversity	0.07	-	0.95	0.13	-	-	-	0.13	0.48	-	-	-	-	0.08	0.67	0.25
Species richness	-	-	0.51	-	-	-	-	-	0.95	-	-	-	-	-	-	-

812

813

814

815

816

817

818

819 **Table S6** Observed and expected values of Moran's I and associated P-values to test for

820 spatial autocorrelation. Tests were based on residuals from the full model for each scale and

821 each species

822
823

Species	Broadscale			Finescale			Combined		
	obs	exp	p	obs	exp	p	obs	exp	p
Lesser Whitethroat	0.014	-0.013	0.073	0.028	-0.013	0.007	0.022	-0.013	0.022
Tree Pipit	0.012	-0.013	0.954	-0.019	-0.013	0.707	-0.015	-0.013	0.886
Dunnock	0.002	-0.013	0.345	0.001	-0.013	0.356	0.004	-0.013	0.272
Chaffinch	0.003	-0.013	0.529	0.008	-0.013	0.166	0.014	-0.013	0.076
Wren	0.003	-0.013	0.518	-0.019	-0.013	0.680	-0.013	-0.013	0.988
Northern Wheatear	0.002	-0.013	0.455	-0.021	-0.013	0.578	-0.020	-0.013	0.619
Water Pipit	0.008	-0.013	0.721	-0.017	-0.013	0.802	0.006	-0.013	0.210
Species diversity	0.020	-0.013	0.646	-0.022	-0.013	0.542	-0.027	-0.013	0.347
Species richness	0.023	-0.013	0.503	-0.016	-0.013	0.849	-0.020	-0.013	0.628

824
825
826
827 There was only a single significant result, for the finescale model for Lesser Whitethroat. In

828 this case, models were re-run accounting for spatial effects by adding a smoothed interactive

829 effect of latitude and longitude in a Generalized Additive Mixed Model using the gamm

830 command in the package gamm4 (Wood & Scheipl 2017). This made no difference to the

831 model outcome in terms of significance levels (Table S6), and parameter estimates were

832 similar. We therefore conclude that for this species, the significant spatial autocorrelation

833 detected did not have an effect on model outcomes.

834
835

836

837

838 **Table S7** A comparison of models predicting Lesser Whitethroat occurrence in relation to

839 finescale habitat variables without (standard model) and with (spatial model) accounting for

840 spatial effects. For variable definitions, see Table 1

841

Variable	Standard model				Spatial model			
	Parameter	SE	z	P	Parameter	SE	z	P
Intercept	-0.711	0.601	-1.183	0.237	-0.887	0.678	-1.130	0.195
H05	0.205	0.274	0.749	0.454	0.058	0.305	0.191	0.849
H1	0.273	0.316	0.874	0.382	0.516	0.368	1.399	0.166
Bilfreq	0.143	0.757	0.189	0.850	0.184	0.827	0.222	0.825
Bilfreq^2	-1.547	1.290	-1.119	0.230	-1.639	1.349	-1.215	0.229
SDshrub	0.025	0.334	0.074	0.941	0.093	0.358	0.259	0.797
Canfreq	-0.059	0.353	-0.168	0.867	-0.158	0.390	-0.450	0.687

842

843
844
845 **Reference**

846

847 Wood S, Scheipl F (2017) Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R

848 package version 0.2-2, URL http://CRAN. R-project. org/package= gamm4

849

850

851
852

The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

Susanne Jähnig[1]*, Riccardo Alba[1], Cristina Vallino[1], Domenico Rosselli[2], Marco Pittarello[3], Antonio Rolando[1] & Dan Chamberlain[1]

[1] Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123, Turin, Italy.
[2] Ente di Gestione delle Aree Protette delle Alpi Cozie, Via Fransuà Fontan 1, 10050 Salbertrand, Italy.
[3] Department of Agricultural, Forest and Food Sciences, University of Turin, Largo Paolo Braccini 2 ,10095 Grugliasco, Italy.

*Corresponding author

Email: susanne.jaehnig@gmail.com

ESM Fig. S1

Relationship between significant model-averaged parameters of the combined model set for bird species richness, diversity and individual bird species. For individual bird species, black circles represent the point counts where a species was present/absent in relation to the relevant variable. The size of the circle is proportional to the number of points for a given category of presence/absence at a particular level of the respective variable. For bird species richness and diversity, black circles represent the H-value (diversity) or the number of bird species (richness) in relation to canopy frequency for a given point count, where the size of the circle is proportional to the number of points for a given H-value (diversity) or species number (richness) at a particular level of canopy frequency.

884
885
886
887
888
889
890
891
892
893
894
895
896
897
898
899
900
901
902
903
904
905
906
907
908
909
910
911
912
913
914
915
916
917
918
919